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RESEARCH ARTICLE

Ontogeny of learning walks and the acquisition of landmark information in desert ants, *Cataglyphis fortis*

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ABSTRACT

At the beginning of their foraging lives, desert ants (*Cataglyphis fortis*) are for the first time exposed to the visual world within which they henceforth must accomplish their navigational tasks. Their habitat, North African salt pans, is barren, and the nest entrance, a tiny hole in the ground, is almost invisible. Although natural landmarks are scarce and the ants mainly depend on path integration for returning to the starting point, they can also learn and use landmarks successfully to navigate through their largely featureless habitat. Here, we studied how the ants acquire this information at the beginning of their outdoor lives within a nest-surrounding array of three artificial black cylinders. Individually marked 'newcomers' exhibit a characteristic sequence of learning walks. The meandering learning walks covering all directions of the compass first occur only within a few centimeters of the nest entrance, but then increasingly widen, until after three to seven learning walks, foraging starts. When displaced to a distant test field in which an identical array of landmarks has been installed, the ants shift their search density peaks more closely to the fictive goal position, the more learning walks they have performed. These results suggest that learning of a visual landmark panorama around a goal is a gradual rather than an instantaneous process.

KEY WORDS: Landmark learning, Navigation, Experience-dependent behavior, Visual landmark, Central place forager, Path integration

INTRODUCTION

The crucial challenge for all central place foragers is to find their way back to their central place, e.g. the nest, successfully after foraging in the nest surroundings (for a review, see Wehner, 1992). In order to return safe and sound, a variety of information relevant for navigation must be detected, learned, memorized and retrieved by the animals in the right place at the right time.

After scavenging for dead insects in their hostile and largely featureless salt pan environment for distances of up to several hundred meters (Buehlmann et al., 2014), desert ants (*Cataglyphis fortis*) must successfully return to their inconspicuous nest entrance. It is this feat of navigation that made *C. fortis*, a prime example of a solitary central place forager, a model organism for navigation (for a review, see Wehner, 2008). The key to the ants' navigational success is path integration (Müller and Wehner, 1988; Wehner, 1982; for a review, see Collett and Collett, 2000).

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The navigational performances of the desert ants become even more impressive if one considers the short time span within which the necessary information must be acquired. After undertaking tasks within the nest for about 4 weeks, the ants forage outside the nest only for less than a week (*Cataglyphis bicolor*: Schmid-Hempel and Schmid-Hempel, 1984). The life expectancy of *C. fortis* outside the nest has not been systematically determined yet, but Ziegler and Wehner (1997) mention 7.3 days (for a short survey comparing the forager survival frequencies of different desert ant species, see fig. 39.1 in Wehner and Rössler, 2013). During the rapid transition from indoor to outdoor life, the workers' behavior as well as its neuronal underpinnings change drastically (Stieb et al., 2010, 2012). In this transition phase, the ants exhibit a distinct behavioral trait, the so-called learning walks, similar to the learning flights described for bees and wasps (for two detailed recent studies, see Philippides et al., 2013; Stürzl et al., 2016). Such learning walks have previously been described for *C. bicolor* (Wehner et al., 2004). In the beginning, the ants perform several exploratory walks meandering around their nest entrance and including frequent body rotations. With increasing experience, the ants stay outside the nest for longer and longer times, and their foraging efficiency as well as their fidelity to a specific foraging sector increases. During the learning walks, the ants do not search for food, but most probably learn about the nest's surroundings (Wehner et al., 2004).

In contrast to their congeneric relatives, *C. fortis* ants occupy a featureless habitat devoid of shrubs or other prominent visual landmarks (Dillier and Wehner, 2004). Even though they are confronted with only a few obvious visual landmarks in their natural environment, and therefore rely predominantly on vector navigation (for a review, see Cheng et al., 2014), many studies have shown their ability to learn and use artificial landmarks successfully (for a review, see Wehner, 2008). It is important to note that landmarks may serve different navigational purposes. They may either help to pinpoint the goal, which may be the nest (Bregy et al., 2008; Knaden and Wehner, 2005; Wehner et al., 1996) or a feeding site (Bisch-Knaden and Wehner, 2003a; Wolf and Wehner, 2000), or guide the foragers *en route* (Andel and Wehner, 2004; Collett, 2010; Collett et al., 1992; Wehner et al., 1996). Furthermore, the ants may link so-called 'local vectors' to specific landmarks (Bisch-Knaden and Wehner, 2001; Collett et al., 1998, 2001). In general, the visual landmark memories of *C. fortis* are very stable and long lasting for up to the entire foraging life span (Ziegler and Wehner, 1997). A landmark memory is most robust when acquired close to the nest entrance (Bisch-Knaden and Wehner, 2003b). These studies consistently show that *C. fortis* uses visual landmarks as navigational aids. In the present study, we show how much experience *C. fortis* desert ants need in order to gather enough information about visual landmarks for finally pinpointing the position of the goal, i.e. the nest. We confronted the ants with an artificial landmark panorama around their nest entrance and designed a two-stage approach to investigate the following two

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aspects. (1) The movements of individually marked ants were analyzed through systematic observation and recording of paths for their entire life span outside the nest. (2) Displacement experiments were used in order to test how exactly the ants located the position of their nest entrance, after they had performed various numbers of learning walks. We found that the ants acquire the information about the landmark panorama around the nest entrance gradually rather than instantaneously.

MATERIALS AND METHODS

Test animals and study site

We performed this study with *Cataglyphis fortis* (Forel 1902) desert ants in the summer of 2014 at a saltpan near Menzel Chaker, Tunisia (34°57′N, 10°24′E). The two different colonies used for the experiment were located towards the middle of the saltpan where almost no natural landmarks in the nest's vicinity occur. The experienced foragers of the ant colonies were marked for 3 days before the experiment started. After this period, we considered all unmarked ants as newcomers, which did not have experience above ground. These individuals were caught and were either tested immediately or marked with a unique multi-color code using car paint (Motip Lackstift Acryl, MOTIP DUPLI GmbH, Haßmersheim, Germany).

Experimental procedure

In order to enable accurate recordings of the ants' paths, we painted a net (10 m×10 m) with diluted wall paint around the nest entrance of each colony (Fig. 1A). The grid had 1 m^2 squares and the inner 4 m^2 around the nest entrance were additionally subdivided with a grid size of 0.2 m. Three artificial landmarks which consisted of black cylinders (height: 38 cm, diameter: 22 cm) were placed at a 2 m distance north (0 deg), southeast (120 deg) and southwest (240 deg) of the nest entrance. The ants were able to leave the nest during the experiment in the daytime, but not in the evening, at night or in the early morning, as we covered the nest entrance. This enabled us to record all appearances of the ants, i.e. all learning walks and foraging trips, outside the nest. Furthermore, we recorded the paths of individual ants as often as possible using squared paper. The last walk of individually marked ants before the test was always recorded. We caught the test animals shortly before they entered their nest. Therefore, the ants' path integrator had been reset to zero ('zero-vector ants'), so that the animals had to rely solely on landmark information when being tested. The distant test field offered a similar array of three artificial landmarks (Fig. 1B). After capture, the ants were immediately transferred in the dark in plastic tubes to the test field. They were released at one of three possible positions to avoid a location-dependent bias. The release points were located 3 m away from the fictive nest position between the landmarks (60, 180 or 300 deg, respectively). After releasing the ant within a plastic ring, we offered a cookie crumb and noted whether the ant picked it up or not. Afterwards, we recorded the ant's path for 5 min. Each ant was tested only once and then removed from the experiment (i) to avoid recapture and (ii) to favor the occurrence of newcomers.

Data analysis

For digitizing the walks, the protocol sheets were scanned with a resolution of 300 dpi. The resulting images were then further processed in a customized application for Android devices written with MIT Appinventor (www.appinventor.mit.edu), which we designed and programmed for this task. Specifically, the scans were loaded into the application running on an Xperia Z2 tablet (Sony, resolution: 1920 pixels×1200 pixels) and the ants' walks were traced on the screen with a tablet pen (Jot Pro Fine Point Stylus, Adonit). With a physical size of 18 cm×18 cm, the representation of the 10 m×10 m grid on the screen was comparable to that on the datasheets, so the digitization procedure did not deteriorate the precision of the data. Before saving the data, the walks could be rotated so as to superimpose the release points. The dataset saved by the application contained both a list of coordinates along the path and a pixel array (200 pixels×200 pixels, 1 pixel=0.05 m) encoding whether the ant crossed a pixel or not. The former was used for a quantitative analysis of the results while the latter was used for creating false color maps.

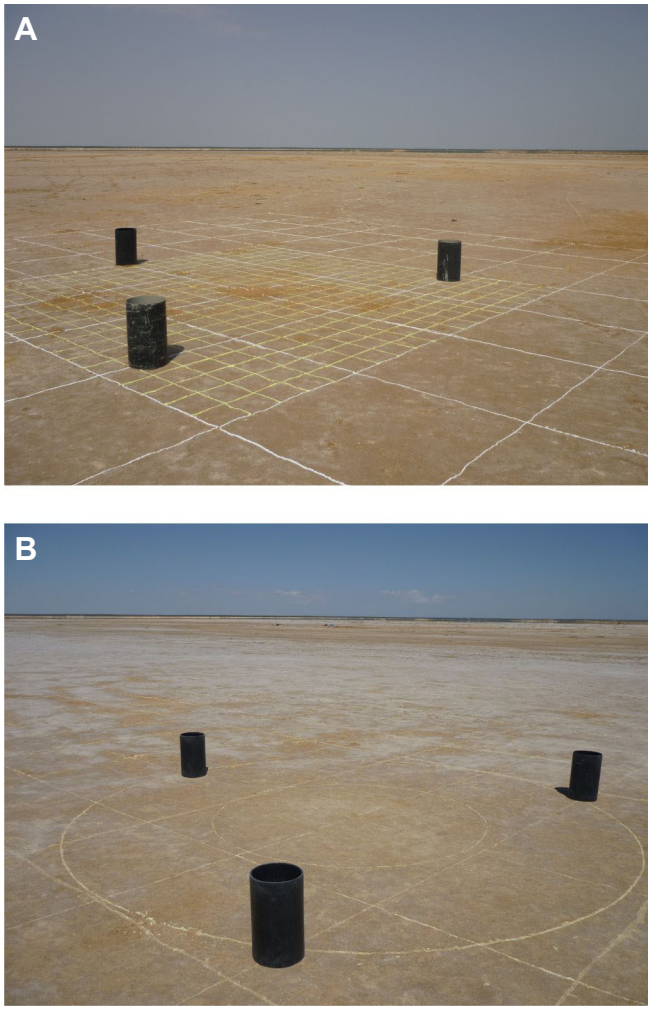

Fig. 1. Two identical landmark arrays. Three artificial landmarks offer a specific panorama at the nest (A) and the test field (B).

Categorization

We categorized the test animals based on the previous individual experience of the ants. (1) For the first category, unmarked ('black') ants were caught and tested after their first appearance, i.e. we considered them to be naive and without any experience in the field. They stayed within a 0.3 m radius around the nest entrance. (2) The second category contained individually marked ants that had performed only short learning walks less than 0.7 m away from the nest. They did not forage. (3) For the third category, we pooled all ants that performed long learning walks or their first foraging trip. These ants had moved more than 0.7 m from the nest before the test.

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However, they did not leave the nest in a straight line, but followed a more circuitous route, including many loops. In this category, learning walks may blend into foraging walks (see e.g. Fig S1G–I). This shows that learning about nest-defining landmarks may continue during the first phase of foraging. (4) In contrast, the experienced foragers in the fourth category moved much faster and ran off in a straight line. They often stayed away for several minutes and usually returned with a food item before being tested. In Fig. S2A, the four categories of experience are correlated with the number of appearances outside the nest. Of course, any segmentation of a phenomenologically continuous process is subject to some degree of arbitrariness. However, as the categorization chosen here correlates very well with the learning success, we feel that the designation of categories 1–4 represents an appropriate approach. (5) The last category contained all ants that we marked before the start of the experiment. These ants were experienced foragers as well, but they first moved within their nest surroundings without the artificial landmark panorama and thus can be considered as 're-learners'. As we do not have any information about the individual history of this group of ants before the test, category 5 might be a rather inhomogeneous group of ants. As such, we include them only for a rough comparison.

Statistics

To compare the five categories of experience regarding the proportion of ants that (i) took a food item on the test field and (ii) directly crossed the fictive nest position during their search on the test field, we used Fisher's exact test (two-sided) with Bonferroni–Holm correction. The significance level was α=0.05.

To compare the ants of different categories with regard to their search performance, we first plotted all searches of one category in a false-color map indicating how many ants crossed any given 0.2 m×0.2 m pixel on the test field. The origin of the false-color map is the fictive position of the nest. We then calculated the median position of the ants' search center from all *x*- and *y*-coordinates. Afterwards, we determined the search center of the groups, which is the median of the individuals' median search positions of one category (see Pfeffer et al., 2015). We compared the search accuracy as well as the search precision of the ants belonging to the different categories with the Kruskal–Wallis test and *post hoc* pairwise comparisons with the Mann–Whitney *U*-test with Bonferroni–Holm correction. The significance level was α=0.05. The 'search accuracy' was defined as the median distance of the individual's search center to the fictive nest position, and the 'search precision' as the median distance of the individual's path to its corresponding search center (see Pfeffer et al., 2015). To evaluate search accuracy and precision, we used only the ants that stayed on the test field for the total time of 5 min. However, all test animals were included in the heat map visualization and the bar graphs. To compare the categories regarding other quantitative aspects (like number of appearances, number of turns and duration of trips outside the nest), we also used Kruskal–Wallis test and *post hoc* pairwise comparisons with the Mann–Whitney *U*-test with Bonferroni–Holm correction. All statistics were performed with Matlab R2014b (MathWorks, Inc., Natick, MA, USA).

RESULTS

At the nest site: ants exhibit a characteristic ontogeny of learning walks before they start foraging

Our long-term observation of what happened at the nest entrance revealed that the behavior of individually identifiable ants changed drastically over time when leaving the nest: with increasing experience (where 'experience' is defined as the number of appearances outside the nest; Fig. S2A), the ants moved further away from the nest entrance in a gradual manner and they did so with increasing straightness (Fig. 2; Figs S1 and S2). Based on these behavioral differences, we categorized the ants into five different categories (see Materials and methods). In the beginning, the ants (category 1; Fig. 2A; Fig. S1A–C) left the nest only for a short period of time (less than a minute; Fig. S2B) and moved a distance of only a few centimeters from the nest (less than 0.3 m). During these first learning walks, the ants were very timid and easily scared. When caught at their first appearance to be marked individually, only four of 42 ants reappeared on the same day. The vast majority, more than two-thirds (27 of 42 ants), returned the next day and started their foraging career then. The remaining test animals reappeared 2 or 3 days after being marked (eight and three ants, respectively). In category 2, the ants made up to four very short learning walks after being marked at their first appearance (Fig. 2B). These learning walks did not take them further than 0.7 m from the nest entrance (median maximal distance from the nest entrance: 0.41 m). With more experience, the ants covered longer distances (category 3; Fig. 2C–E; Fig. S1D–H). Nine of the 15 ants in category 3 left the nest field before being captured for the test (Fig. S2C). The remaining six ants moved a few meters from the nest (median maximal distance from the nest: 2.18 m). The characteristics of all these further learning walks were relatively slow movements and winding paths. The ants of category 3 had significantly less-straight paths than the experienced foragers (Fig. S2D). Furthermore, these paths included full-turns frequently and significantly more often than the paths of experienced foragers (in category 3 and 4, the median number of turns per run was eight and one, respectively; Mann–Whitney *U*-test: category 3 versus 4, $z=-3.571$, $N_3=15$, $N_4=20$, $P<0.05$). These turns occurred particularly in the beginning of the ants' outbound trip (see examples in Fig. 2 and Fig. S1). During the learning walks, ants seemed to explore the full range of azimuthal directions (though it was not possible to analyze dominant axes of the trajectories in detail; examples are given in Fig. 2E and Fig. S1D–F). If the ants came across a food item on the nest field, they returned to their nest in a straight line (Fig. 2D,F). The ants needed at least three appearances outside the nest before they abandoned their orientation behavior and started foraging successfully (Fig. S2A). However, some ants made up to seven extensive learning walks (category 3). Their paths straightened with increasing experience (an example is given in Fig. S1G–I). Usually, the ants started to forage around their second day outside the nest, then they disappeared from the nest field in the saltpan and left the nest for several minutes. The duration of the outbound trips increased significantly from category 1 to category 4 (Fig. S2B). Experienced foragers (category 4) generally left the nest field and returned to the nest in a straight line (Fig. 2F, green paths).

In the test field: increasing numbers of learning walks improve the accuracy of pinpointing the goal

The test animals were captured close to their nest entrance at different stages of experience and afterwards released in the distant test field. There, a landmark array identical to the one surrounding the nest entrance was set up. As the ants were devoid of any vector information (zero-vector ants), they had to rely solely on the landmarks when searching for the nest. A look at the search paths of individual ants reveals the main result: naive ants and ants with only a little experience (category 1 and 2, respectively) immediately searched at the release point (category 1, Fig. 3A, and category 2,

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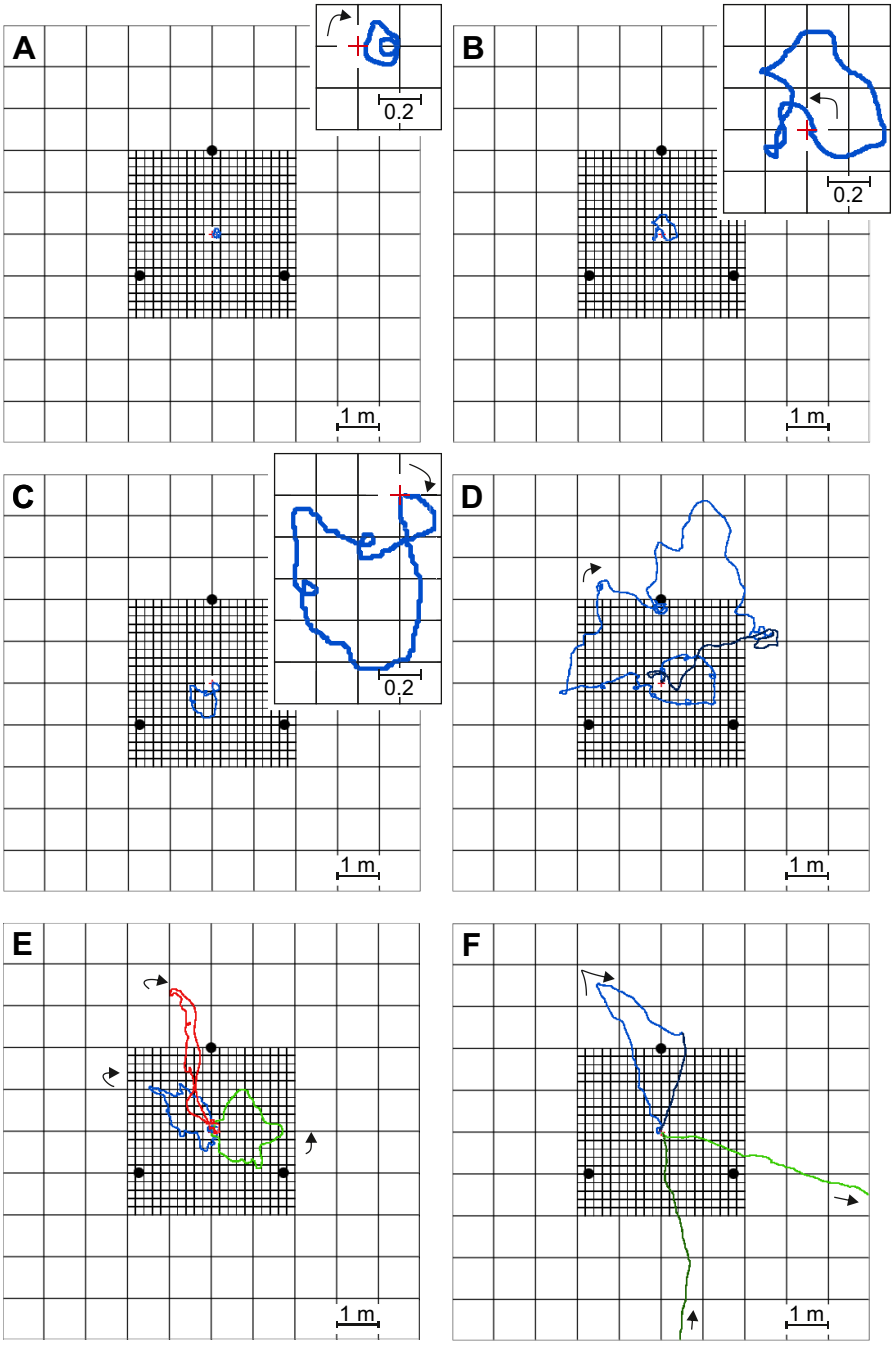

Fig. 2. Ontogeny of learning walks. (A) First learning walk of a naive ant (category 1). (B) Second learning walk of another ant (category 2). (C) Third and (D) fourth walk of another individual (category 3). (D) This ant found food for the first time before being tested (light blue: outbound walk, dark blue: homeward run after finding a food item). (E) Three successive learning walks of another ant (no. 4 – blue, no. 5 – green and no. 12 – red) and its (F) first (light blue: outbound walk, dark blue: homeward run after finding a food item) and last foraging trip (light green: outbound run, dark green: homeward run) (category 4). The nest entrance is located in the middle of the landmark array (+) and surrounded by three landmarks (black filled circles). The grid size corresponds to 1 m on the nest field (the inner 4 m×4 m are additionally subdivided into 0.2 m×0.2 m boxes). The insets in A–C show the short paths at higher magnification (grid size corresponds to 0.2 m). The black arrows show the direction of the ants' paths.

Fig. S3A–C), whereas experienced foragers directly proceeded to the fictive nest entrance position, where they started searching for their nest (category 4, Fig. 3C and Fig. S3G–I). Ants that had made long learning walks or had finished their first foraging trip before being tested (category 3) proceeded towards the fictive nest position in the middle of the landmark array, and their search was centered in between the release point and the fictive nest position (Fig. 3B; Fig. S3D–F).

Integrating the ants' searching paths of either category into false-color maps (Fig. 3D–F; Fig. S4) illustrates the results more impressively. With increasing experience in the nest area, the ants shifted their search centers more from the point of release toward the fictive position of the nest entrance (Fig. S5). Calculating the accuracy (Fig. 4A) and the precision (Fig. 4B) of the ants' searches allowed for statistical comparison of the groups, which revealed significant differences between them (Kruskal–Wallis test: search accuracy, χ_4^2=310,68, N=54, P<0.001; search precision, χ_4^2=14,42, N=54, P=0.007). Naive ants (category 1) and inexperienced ants (category 2) mainly focused their searches around the point of release (Fig. 3D; Fig. S4A; Mann–Whitney U-test with Bonferroni–Holm correction: category 1 versus 2, z=−0.888, N_1=12, N_2=7, P=0.375). Therefore, the distance between the fictive position of the nest entrance and their search centers was large and, consequently, the search accuracies differed from those of the more experienced foragers, which searched closer to the fictive nest entrance position (Mann–Whitney U-test with Bonferroni–Holm correction: category 1 versus 4, z=4.22, N_1=12, N_4=15, P<0.005; 1 versus 5, z=3.48, N_1=12, N_5=11, P<0.006; 2 versus 4, z=3.60, N_2=7, N_4=15,

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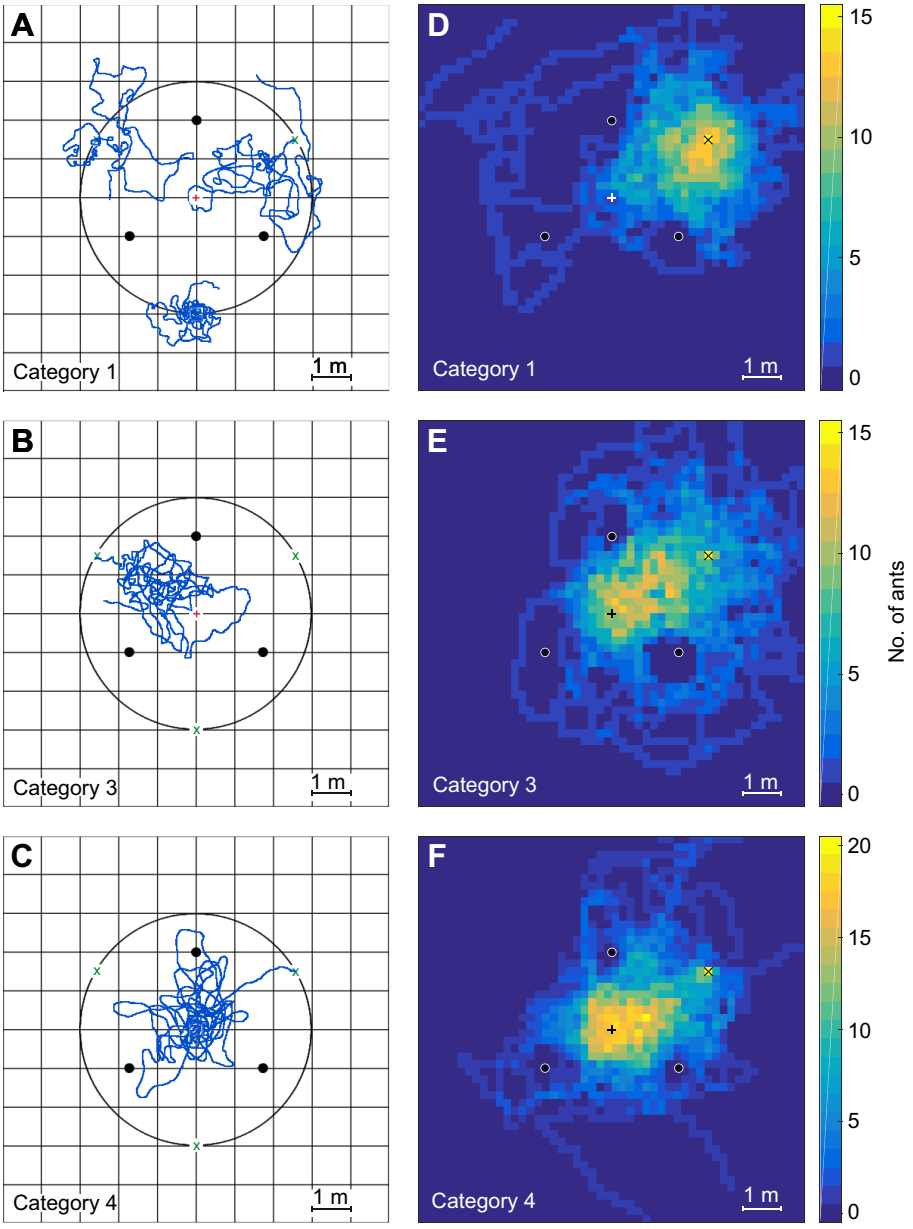

Fig. 3. Examples of searching paths on the test field and false-color maps of ants in three categories of experience. (A–C) Searching paths of three naive ants (category 1; A), an ant with more experience (category 3; B) and an experienced forager (category 4; C). (D–F) Superimposed searching paths of all ants in category 1 (naive ants, *N*=15; D), category 3 (ants that made long learning walks or their first foraging run, *N*=15; E) and category 4 (experienced foragers, *N*=20; F). The fictive position of the nest entrance is located in the middle of the test field (+) surrounded by an identical landmark array to that at the nest (black filled circles). The release points (×) lie 3 m from the fictive nest entrance position. The grid size in A–C corresponds to 1 m on the test field. Each pixel of the false-color map in D–F is equivalent to a 0.2 m×0.2 m square on the test field. Dark blue pixels have not been visited by any ant, whereas yellow indicates that all ants of a category crossed the pixel (the number of test ants for each corresponding color is given next to the color bar).

P<0.005; 2 versus 5, z=3.08, N_2=7, N_5=11, P<0.007). With increasing experience (category 3), the ants searched between the point of release and the fictive nest entrance position (Fig. 3E). Their search accuracy was not significantly different from that of the other groups (Mann–Whitney U-test with Bonferroni–Holm correction: category 1 versus 3, z=2.60, N_1=12, N_3=9, P=0.010; 2 versus 3, z=2.44, N_2=7, N_3=9, P=0.015; 3 versus 4, z=2.21, N_3=9, N_4=15, P=0.028; 3 versus 5, z=1, N_3=9, N_5=11, P=0.288). All experienced foragers (categories 4 and 5) concentrated their searches around the fictive nest entrance position (Fig. 3F; Fig. S4B). There was no significant difference between the search accuracies of ants that had learned only the artificial landmark array and those that had already foraged prior to the installation of the landmarks and hence had to re-learn the panorama around the nest (Mann–Whitney U-test with Bonferroni–Holm correction: category 4 versus 5, z=−0.83, N_4=15, N_5=11, P=0.407). All categories showed similar search precision, ranging from 0.5 to 1.4 m (Fig. 4B). The groups did not differ significantly when compared pairwise (Mann–Whitney U-test with Bonferroni–Holm correction: category 1 versus 2, z=0, N_1=12, N_2=7, P=1; category 1 versus 3, z=−2.45, N_1=12, N_3=9, P=0.015; category 1 versus 4, z=−2.22, N_1=12, N_4=15, P=0.027; category 1 versus 5, z=−2.49, N_1=12, N_5=11, P=0.013; category 2 versus 3, z=−2.11, N_2=7, N_3=9, P=0.035; category 2 versus 4, z=−2.32, N_2=7, N_4=15, P=0.020; category 2 versus 5, z=−2.08, N_2=7, N_5=11, P=0.038; category 3 versus 4, z=1.20, N_3=9, N_4=15, P=0.233; category 3 versus 5, z=0.23, N_3=9, N_5=11, P=0.820; category 4 versus 5, z=−1.34, N_4=15, N_5=11, P=0.178).

Experienced foragers (categories 4 and 5) were most successful in carrying food items homeward. Two measures illustrate their success in particular. First, with increasing experience, the ants were more likely to take a cookie crumb after being released on the test field than those with less experience (Fig. 5A). Naive ants (category 1) took a cookie crumb significantly less often than experienced foragers (Fisher's exact test with Bonferroni–Holm correction: category 1 versus 4, P<0.0055; 1 versus 5, P<0.005). The

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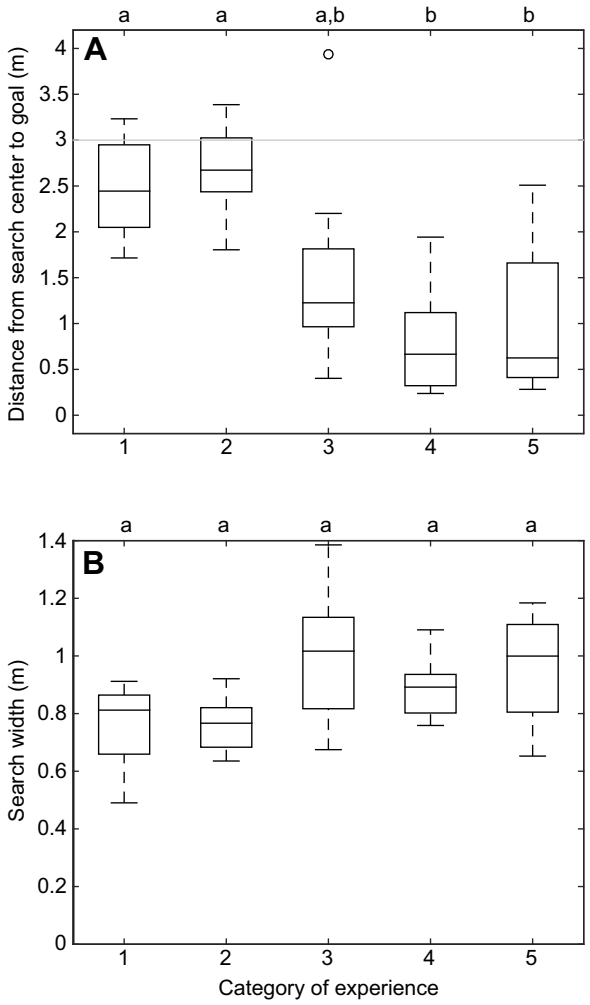

Fig. 4. Search accuracy and search precision of the ants in the five categories of experience. (A) Search accuracy was calculated as the distance between the search center and goal. (B) Search precision is the distance from the path to the search center (i.e. search width). The central mark is the median, the edges of the boxes are the 25th and 75th percentiles, and the whiskers extend to the most extreme data points (excluding outliers). Outliers are plotted individually as circles. Number of ants: category 1, *N*=12; category 2, *N*=7; category 3, *N*=9; category 4, *N*=15; and category 5, *N*=11. Different letters indicate significant differences between the groups (*post hoc* Mann–Whitney *U*-test with Bonferroni–Holm correction; for details see Results).

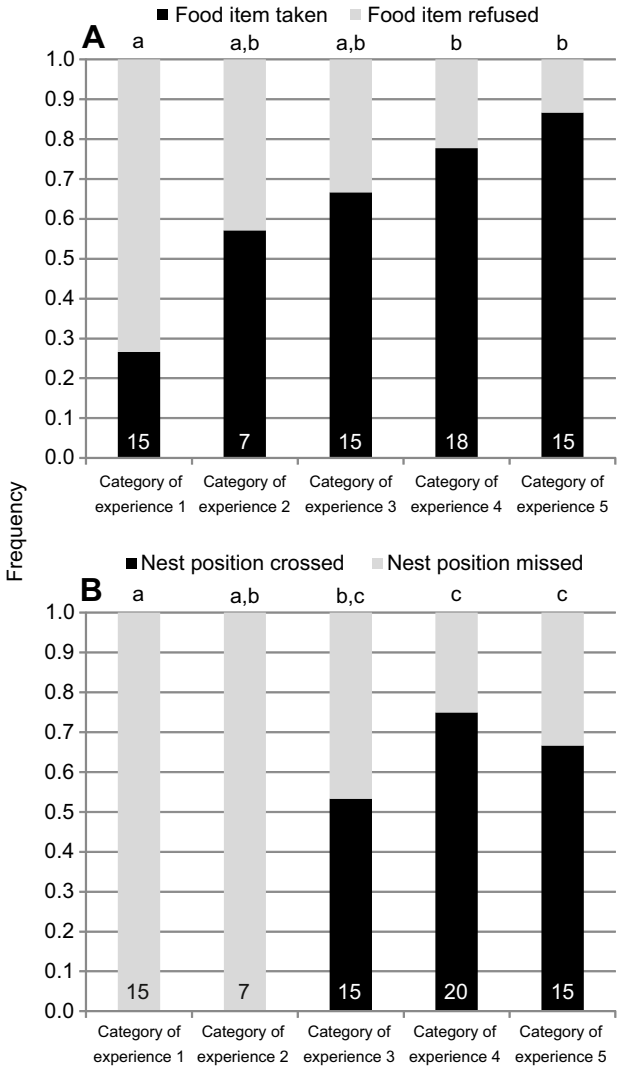

Fig. 5. Foraging success. Proportion of ants that (A) took a cookie crumb and (B) crossed the fictive nest position in the test field. Number of ants (*N*) is shown in the bars. Different letters indicate significant differences between the categories (Fisher's exact test with Bonferroni–Holm correction; for details see Results). The number of tested ants is given in parentheses (for two ants in category 4, it was not clear whether a crumb was taken or refused).

proportion of ants picking up a food item increased from category 1 to 5, but these differences were not significant between the other groups when compared pairwise (Fisher's exact test with Bonferroni–Holm correction: category 1 versus 2, P=0.343; category 1 versus 3, P=0.066; category 2 versus 3, P=1; category 2 versus 4, P=0.356; category 2 versus 5, P=0.275; category 3 versus 4, P=0.697; category 3 versus 5, P=0.390; category 4 versus 5, P=0.665). Second, with increasing experience, the ants were more likely to cross the fictive position of the nest on the test field (Fig. 5B). Only very few ants of categories 1 and 2 came close to the fictive position of the nest entrance (category 1, Fig. 3D and category 2, Fig. S4A; for an example of an individual path, see Fig. 3A ant starting at the northeast release point). However, even these ants never crossed the fictive nest entrance position and, hence, the results were significantly different from those of the more experienced foragers (Fisher's exact test with Bonferroni–Holm correction: category 1 versus 3, P<0.007; 1 versus 4, P<0.005; 1 versus 5, P<0.005; 2 versus 4, P<0.006; 2 versus 5, P<0.008). The increase in the number of ants crossing the fictive nest entrance from category 2 to 3 was visible, yet not statistically significant (category 2 versus 3, P=0.023). In addition, there were no significant differences between the proportion of ants reaching the fictive nest entrance in categories 3, 4 and 5 (category 3 versus 4, P=0.283; 3 versus 5, P=0.711; 4 versus 5, P=0.712).

DISCUSSION

The ants' rapid transition from intranidal workers to extranidal foragers offers the opportunity to comprehensively record the ants' first spatial activities outside the nest – the sequence of learning walks – and the subsequent foraging journeys, ideally throughout the ants' entire foraging lives. Here, we have taken this opportunity to investigate how the ants' accuracy in local visual homing increases with the number of learning walks performed by the ants around the nest entrance. We show that the number of learning

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walks, the distance by which the ants move away from the nest entrance during the learning walks and the accuracy with which they subsequently pinpoint the nest site are strongly correlated.

Cataglyphis fortis exhibits a characteristic ontogeny of learning walks

Several studies have investigated the learning flights of bees and wasps and the learning walks of ants at their nests or feedings sites (honeybees: Becker, 1958; Vollbehr, 1975; Lehrer, 1991, 1993; Capaldi and Dyer, 1999; bumblebees: Hempel de Ibarra et al., 2009; wasps: Zeil, 1993a, 1993b; Stürzl et al., 2016; wood ants: Judd and Collett, 1998; Nicholson et al., 1999; desert ants: Müller and Wehner, 2010). However, only very few studies have specifically described the ontogeny from the start of learning walks or flights at the beginning of the forager's career to the foraging trips of experienced foragers (desert ants: Wehner et al., 2004; honeybees: Capaldi et al., 2000; Degen et al., 2015; bumblebees: Osborne et al., 2013). The first learning walks and flights all share some common features: when leaving the nest for the first time, the animals meander around the nest entrance including circular movements or rotations in their trajectories. These motion sequences were described in great detail for the first time in solitary wasps (Zeil, 1993a). Since then, similar observations have been made for other species (desert ants: Müller and Wehner, 2010; bumblebees: Philippides et al., 2013). Usually, the newcomers explore the nest's surroundings without bringing back any food items. This distinction between the learning and foraging phase is not as clear in bumblebees as it is in honeybees and ants, because the former occasionally bring home pollen after their first trip outside the nest (Hempel de Ibarra et al., 2009; Osborne et al., 2013). With increasing experience, the bees' maximal range, distance traveled, area covered and ground speed increase significantly (honeybees: Capaldi et al., 2000; Degen et al., 2015; bumblebees: Hempel de Ibarra et al., 2009). Desert ants (*C. bicolor*) also stay longer outside the nest with more experience. They cover longer distances and they forage more efficiently. Furthermore, after exploring all directions during their learning walks, successful *Cataglyphis* ants preferentially stick for a considerable foraging time to one sector (Wehner, 1987; Wehner et al., 2004). Some basic features in the structure of *C. fortis*' learning walks have been described before (Stieb et al., 2012). Our constant and long-term observations close to the nest entrance confirm and extend these findings. We demonstrate that *C. fortis* ants undergo a distinct ontogeny of their learning walks until they become foragers when confronted with an artificial landmark panorama. The learning walks in the beginning of the desert ants' foraging life are slow, more twisted and much shorter than the foraging runs of experienced ants. With increasing experience, the ants move further away from the nest and eventually start foraging. The next step will be to examine the learning walks around the nest entrance by using high-speed video analyses, in order to analyze the fine structure of the walks in more detail. A recent computational study showed that successful orientation is best achieved with a large visual field and low resolution (Wystrach et al., 2015). Interestingly, *C. fortis*' visual field covers a huge area (about 93%) of the unit sphere and remains constant with varying body size of the ants, whereas the number of ommatidia, and hence the resolution of the compound eyes, varies with different body and thus eye sizes (Wehner, 1983; Wehner et al., 2014; Zollikofer et al., 1995). Therefore, *C. fortis* meets the conditions of a visual system that is evolutionarily optimized for navigation by panoramic landmark cues.

Landmark learning requires stable memory formation

In the beginning of their foraging lives, ants – and other insects – must adjust their orientation systems and acquire various kinds of visual information (for a review, see Zeil, 2012). Outside the nest, they have to learn possible landmark cues around their home, and they have to calibrate their celestial compass. Here, we used an artificial landmark panorama to show that the desert ants' learning walks are crucial prerequisites for successful homing. After only three to seven appearances and learning walks outside the nest, *C. fortis* starts to forage. The ants' rapid transition from a naive newcomer performing a few learning walks to an experienced and successful forager is thus another example of the impressive speed of navigational learning in insects with short (foraging) life spans (Collett, 1998). Intriguingly, the same amount of time that the ants need to perform their learning walks, i.e. usually 2–3 days, is necessary after first exposure to light pulses to induce neuronal changes in visual subregions of the mushroom bodies of *C. fortis* (Stieb et al., 2010, 2012). A recent computational study revealed that the desert ant mushroom body circuit has the capacity to store hundreds of independent images taken by an ant during its outbound trip, and to distinguish these from other deceptive, yet very similar images when looking off-route (Ardin et al., 2016). Formation of long-term memory (LTM) requires at least 1 day (early LTM), and 3 days (late LTM) to be consolidated as a stable LTM (for review, see Menzel, 2001). Studies in honeybees (Hourcade et al., 2010) and in leaf-cutting ants (Falibene et al., 2015) show that the formation of transcription-dependent, stable olfactory LTM is associated with structural synaptic changes in olfactory subregions of the mushroom bodies after 2–3 days. Hence, we hypothesize that the duration of the learning walks performed by the ants at the beginning of their foraging lives is correlated with the time needed to establish a robust LTM of stable nest surroundings, which in turn is necessary for successful homing.

Naive newcomers are not yet in foraging mood

Experienced foragers picked up a cookie crumb on the test field significantly more often than naive newcomers did. This difference in behavior certainly reflects the ants' motivational state of foraging. It has been shown before that navigational states can influence the motivation to perform other kinds of behavior. For example, if *C. fortis* ants are repeatedly forced to return to the nest guided exclusively by landmarks and hence to put their path integrator into an unusually large negative state, they drop their cookie crumb and express largely reduced escape behavior when approached by the experimenter (Andel and Wehner, 2004). Furthermore, the state of the path integrator can control the state of aggressiveness of *C. fortis*: zero-vector ants showed higher levels of aggressiveness than ants that had run off only a quarter of their home vector (Knaden and Wehner, 2004). Additionally, motivational state may determine whether an ant continues its trip inward or outward: Australian desert ants (*Melophorus bagoti*) link their route memories to inbound or outbound states of their foraging excursions, and these states may determine whether or not the ants retrieve their route memories (Wehner et al., 2006). Furthermore, wood ants (*Formica rufa*) choose different routes depending on their feeding state – if fed, they choose the homeward pattern, whereas unfed ants follow the route with the foodward pattern (Harris et al., 2005). Remarkably, landmark cues can also change the desert ants' motivation from homing to foraging. If *C. fortis* is disturbed on its way to a feeder, it usually returns to its nest. However, if landmarks are available to guide the ants to a familiar feeder, they continue their outbound trip (Merkle and

Wehner, 2008). In our experiment, all ants were motivated to return to the nest. However, experienced foragers were willing to accept food items when released on the test field, whereas less experienced ants refused food items and returned to their nest immediately. Hence, the ants' motivation to forage is dependent on their previous experience and may indicate their confidence in the ability to relocate the nest successfully.

With increasing experience, desert ants locate their goal more accurately and precisely

In most cases, experienced foragers pick up a food item, run straight into the middle of the landmark array and center their search on the test field around the fictive nest entrance (Cheng et al., 2014; Wehner and Räber, 1979; Wehner et al., 1996). In contrast, naive ants search at the release point. If desert ants are lost, they pursue a systematic search strategy. Their search pattern consists of several loops in all azimuthal directions starting and ending at the origin, i.e. the place where the ants presume the nest position to be (*Cataglyphis*: Müller and Wehner, 1994; Wehner and Srinivasan, 1981; *M. bagoti*: Schultheiss and Cheng, 2011). This symmetric search pattern was observed in our study as well (Fig. 3A–C; Fig. S3). All ants exhibited similar search widths, and there was not a significant difference between the categories of experience in regard to their search precision. In contrast, there are clear differences between the categories of experience with respect to search accuracy. The more experienced the ants are, the closer they search to the fictive position of the nest entrance (Figs 3, 4A; Fig. S3–S5). This shows that the ants have learned the landmarks and use the landmark information to search for the nest. Moreover, the increase of search accuracy from naive ants to experienced foragers does not occur instantaneously. If the learning process were instantaneous, ants in category 3 would split into two groups, namely (i) ants that have already learned the landmark panorama and (ii) ants that have not. However, with more experience, the ants shift their searches towards the fictive position of the nest entrance. Ants of category 3 searched at intermediate positions (see Fig. 3B,E; Fig. S3D–F), indicating a gradual (or stepwise) improvement of their learning success.

Novel learning and re-learning exhibit similar characteristics

The gradual acquisition of visual cues by desert ants orientating with artificial landmarks has been previously shown in re-learning paradigms. In these experiments, experienced foragers were confronted with an altered environment and consequently had to adapt their behavior to the new conditions. Faced with an artificial landmark array consisting of four cylinders, the Australian desert ant *M. bagoti* gradually increased its search performance for the nest on a test field when trained with a different number of trials over different numbers of days (Narendra et al., 2007). As *C. fortis* did in our replacement experiment, the proportion of ants crossing the fictive nest entrance between the landmarks increased with more experience (Narendra et al., 2007). Furthermore, the search time of the Namibian desert ant (*Ocymyrmex robustior*) until entering the nest decreased significantly from day to day when the entrance of a nest in a landmark-free environment had been furnished with two artificial cylinders (Wehner and Müller, 2010). As we found with our category 5 ants, and as a number of previous experiments (*C. bicolor*: Wehner and Räber, 1979; *C. fortis*: Wehner et al., 1996; *M. bagoti*: Narendra et al., 2007; for a review, see Cheng et al., 2014) have shown, desert ants can use artificial landmarks for orientation successfully, even if they had learned the natural surroundings of their nest before. Our observations suggest that the behavioral patterns exhibited during the acquisition as well as the recall of landmark orientation show striking similarities between new learners and re-learners. Future studies should investigate these similarities in more detail and examine whether specific sections of learning walks (e.g. the characteristic and frequent turns) are necessary prerequisites for the learning process, as has been shown recently in the learning flights of wasps (Stürzl et al., 2016). Furthermore, it will be interesting to investigate the interplay of the landmark learning and the initial calibration of the celestial compass that must happen at the same time. In addition, detailed neurobiological studies, preferably using the same animals that have participated in landmark learning paradigms, may help to us to understand the neuronal processes underlying the novel learning and re-learning behavioral traits.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

R.W. and W.R. led the study. R.W. and P.N.F. designed the experiment. P.N.F. and M.C. conducted the experiment. P.N.F. and V.L.M. designed and programmed the app for data analysis. P.N.F., M.C. and V.L.M. analyzed the data. P.N.F. wrote the manuscript, and R.W. and W.R. revised the manuscript. All authors participated in discussing the results and checking the paper.

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Supplementary information

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